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Title: Perching but not foraging networks predict the spread of novel foraging skills in starlings

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Corresponding Author: Dr. Neeltje J. Boogert, PhD

Corresponding Author's Institution: University of St. Andrews

First Author: Neeltje J. Boogert, PhD

Order of Authors: Neeltje J. Boogert, PhD; Glenna F Nightingale, PhD; William Hoppitt, PhD; Kevin N Laland, PhD

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Perching but not foraging networks predict the spread of novel foraging skills in starlings

Abstract

The directed social learning hypothesis suggests that information does not spread evenly through animal groups, but rather individual characteristics and patterns of physical proximity guide the social transmission of information along specific pathways. Network-based diffusion analysis (NBDA) allows researchers to test whether information spreads following a social network. However, the explanatory power of different social networks has rarely been compared, and current models do not easily accommodate random effects (e.g. allowing for individuals within groups to correlate in their asocial solving rates). We tested whether the spread of two novel foraging skills through captive starling groups was affected by individual- and group-level random and fixed effects (i.e. sex, age, body condition, dominance rank and demonstrator status) and perching or foraging networks. We extended NBDA to include random effects and conducted model discrimination in a Bayesian context. We found that social learning increased the rate at which birds acquired the novel foraging task solutions by 6.67 times, and acquiring one of the two novel foraging task solutions facilitated the asocial acquisition of the other. Surprisingly, the spread of task solutions followed the perching rather than the foraging social network. Upon acquiring a task solution, foraging performance was facilitated by the presence of group mates. Our results highlight the importance of considering more than one social network when predicting the spread of information through animal groups.

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Introduction

Recent years have seen an explosion of both scientific and public interest in animal innovation and social learning. The behavioural innovations of one individual can rapidly spread through a group of animals through social learning, leading to the establishment of cultural variation across populations (Allen et al. 2013; Hoppitt & Laland 2013). Social learning allows, for example, vervet monkeys to avoid toxic food (van de Waal et al. 2013), meerkat pups to eat scorpions (Thornton & McAuliffe 2006), warblers to mob nest-parasitic cuckoos (Davies & Welbergen 2009), and children to solve complex puzzle boxes (Dean et al. 2012). The origin and social transmission of information thus have major ecological and evolutionary consequences (Avital & Jablonka 2000; Hoppitt & Laland 2013).

Historically, animal social learning was studied primarily by testing whether relatively artificial behaviour patterns could be transferred between demonstrator-observer dyads confined to small enclosures in captivity, often with the objective of seeking to establish whether animals were capable of human-like imitation (Galef 1988; Whiten & Ham 1992; Hoppitt & Laland 2013). However, recent advances in statistical tools now allow researchers to identify social learning when it occurs in more naturalistic social settings in captivity and in animal populations in the wild (Franz & Nunn 2009; Hoppitt et al. 2012; Hoppitt & Laland 2013). Furthermore, these natural(istic) test conditions allow test subjects a free choice of whom to interact with, which in turn might affect whom they are most likely to copy.

Almost two decades ago, Coussi-Korbel and Fragaszy (1995) introduced the concept of "directed social learning", which occurs when social information does not spread evenly through a group. Instead, demonstrator and observer characteristics, such as sex, age, and

50 social rank, affect the salience of demonstrators to observers and the likelihood that social
51 transmission of information occurs between them. Various studies on (semi-)natural animal
52 groups have provided evidence for directed social learning (Hoppitt & Laland 2013). For
53 example, captive groups of chimpanzees exposed to two demonstrators copied the older, more
54 dominant and previously successful model more than the younger, subordinate and
55 experimentally naïve model (Horner et al. 2010). Although demonstrator characteristics did not
56 appear to affect social learning tendencies in captive flocks of blue tits, subordinate males were
57 more likely to acquire a novel foraging skill socially than were dominant males, and juvenile
58 females were twice as likely to socially learn as compared to all other flock members (Aplin et
59 al. 2013). Young female chimps spent more time watching their mothers and learned to fish for
60 termites at an earlier age than young males (Lonsdorf et al. 2004). No sex differences in social
61 learning were found in wild meerkats, but pups and juveniles were more likely than adults to
62 join demonstrators and scrounge from them, and learned to obtain food from a novel foraging
63 task as a result (Thornton & Malapert 2009).
64 The latter study suggests that demonstrators' social tolerance of, and physical proximity
65 to, naïve observers might affect the latters' access to information regarding novel foraging
66 techniques. Coussi-Korbel and Fragaszy (1995) hypothesized that patterns of group members'
67 physical proximity to each other in time and space would predict the pattern of information
68 spread through the group, as well as the similarity to the demonstrator's behaviour achieved by
69 the observer (Coussi-Korbel & Fragaszy 1995). Researchers can now formally test this
70 hypothesis using network-based diffusion analysis (NBDA), pioneered by Franz and Nunn (2009)
71 and extended by Hoppitt et al. (2010) and Nightingale et al. (in press). Using NBDA, novel

72 foraging skills or novel foraging patch discoveries have been shown to spread following the
73 social network in for example tits (Aplin et al. 2012), three-spined sticklebacks (Atton et al.
74 2012; Webster et al. 2013), squirrel monkeys (Claidière et al. 2013), and humpback whales
75 (Allen et al. 2013). However, social networks did not predict the spread of information in
76 captive starlings (Boogert et al. 2008), wild ring-tailed lemurs (Kendal et al. 2010) or redfronted
77 lemurs (Schnoell & Fichtel 2012).

78 One potential methodological reason that NBDA has generated negative findings is that
79 researchers adopting NBDA have thus far always relied on a single social network in their
80 analyses. Kendal et al. (2010) pointed out that it is crucial to use a social network that is
81 relevant to the skill to be socially transmitted, and suggested that a foraging network might
82 have predicted the spread of a novel foraging skill in wild ring-tailed lemur groups better than
83 the non-foraging spatial proximity network adopted in their study (Kendal et al. 2010). Similarly,
84 the studies by Boogert et al. (2008) and Schnoell and Fitchel (2012) each used a single social
85 network based on physical proximity and affiliative interactions, respectively, to predict the
86 spread of novel foraging task solutions, instead of a potentially more relevant foraging network.
87 The suggestion that social networks constructed using different behavioural measures might
88 not be strongly correlated was recently confirmed by a study on wild chacma baboons: Castles
89 and colleagues (in press) compared five different social networks constructed from two
90 interaction and three proximity sampling methods, and found them to be uncorrelated at both
91 individual and network levels (Castles et al., in press). However, to our knowledge no published
92 study has compared the performance of different social networks in predicting the spread of
93 novel foraging skills in animal groups. Furthermore, individual-level characteristics that might

affect directed social learning, such as dominance, age and sex, have rarely been taken into account in NBDA until now.

In the present study, we tested which individual characteristics and social networks explained the patterns in which novel foraging skills spread through small groups of starlings held in captivity. We measured the foraging and perching networks, as well as the foraging and perching dominance ranks, for each of four starling groups composed of wild-caught juvenile and adult females and males. We then trained one subordinate and one dominant starling from each group to solve a novel foraging task using alternate actions and options. Once these demonstrators were trained, they and their group mates were presented with multiple replicates of the novel foraging task, and we scored who solved the task using which of the two task solutions, when and how. To analyse our data, we used our recent extension of NBDA (Nightingale et al., in press) to incorporate individual- and group-level random effects (i.e. allowing for the fact that individuals might be correlated in their rate of solving), alongside individual-level fixed effects (i.e. solvers' sex, age, body condition, social ranks) and performed model discrimination in a Bayesian context. Surprisingly, our results show that the spread of the novel foraging task solutions followed the perching rather than the foraging network, and individual characteristics did not seem to affect the diffusions.

Materials and Methods

Subjects

Experimental subjects were 36 European starlings (*Sturnus vulgaris*), of which 13 were adult males, 13 were juvenile males (hatched in the year of catching) and 10 were juvenile females. We caught these starlings in Finstown on the Orkney Islands on October 1st 2011 using a clap

net, and the lack of adult females in this single catch is likely to be random (wild starling flocks are not known to have obvious sex/age biases in composition). Upon capture, we recorded each starling's age (juvenile or adult), sex, weight and wing length, and fitted each bird with a unique British Trust for Ornithology metal ring. We transported birds to the University of St. Andrews on the day of capture. Upon arrival in St. Andrews, we gave each starling a unique combination of coloured plastic rings (A.C. Hughes), and randomly allocated it to one of four indoor enclosures, resulting in groups of 10, 9, 9 and 8 birds, respectively. Each enclosure measured 3 x 1.20 x 2.30 m and was fitted with full-spectrum fluorescent lights, sawdust and hay bedding, and a large bird bath (76 x 45 x 9 cm). Rope perches and branches spanned the length and height of the enclosure, respectively, and provided at least 7 m of perching space, allowing all birds to perch without being within pecking distance of each other. Softened high-protein dog kibble in 28 cm diameter saucers was available at libitum except for the duration of the diffusion experimental trials (see below). Trays containing dried mealworms hidden in grit were provided regularly to encourage natural foraging behaviours. All food was presented on the floors of the enclosures. Enclosures were kept at 20 ± 1^{o}C with lights on at 0700 and off at 1900 hours.

Association patterns

Foraging associations

We filmed each starling group for four days between November 22nd and December 3rd 2011. For each of these recording days we analyzed 45 min of normal foraging activity by scoring the identity of the birds foraging and the time at which each individual's foraging bout started and ended. To create the foraging association matrix, we first summed the total amount of time that each pair of birds (e.g. birds *i* and *j*) was observed to be foraging simultaneously (F_{ij}). We then summed the total amount of time that each bird was foraging regardless of who else was foraging at the same time (F_{iT}). We created an asymmetric foraging association matrix **F**, in which the foraging association of bird *i* with bird *j* was F_{ij} / F_{iT}, which represents the proportion of *i*'s foraging time spent in the foraging presence of *j*. Likewise, the foraging association of bird *j* with bird *i* was F_{ji} / F_{jT}

149

150 Perching associations

151 We scan-sampled each starling group 100 times between November 10th and December 21st
152 2011 by observing the birds through a small peephole in an opaque curtain that was
153 permanently attached to the front of the enclosure. During each scan sample, we recorded
154 which, if any, individuals were sitting within pecking distance of each other for at least 5 s. Scan
155 samples of the same group were separated by at least 30 min to ensure that consecutive scan
156 samples could be considered to be independent of each other. To create the perching
157 association matrix, we first summed the total number of times each pair of birds (e.g. birds *i*
158 and *j*) was observed to be sitting within pecking distance across the 100 scan samples (P_{ij}). We
159 then summed the total number of times each starling was observed to be sitting within pecking
160 distance of any other group member (P_{iT}). We created an asymmetric perching association
161 matrix **P** in which the perching association of bird *i* with bird *j* was P_{ij}/P_{iT}. This represents the
162 proportion of perching events in which bird *i* was observed to perch within pecking distance of
163 bird *j*, given that *i* was within pecking distance of at least one bird. Likewise, the perching
164 association of bird *j* with bird *i* was P_{ji}/P_{jT}.

165

166

167 *Dominance*

168

169 Foraging ranks

170 To assess dominance ranks in a foraging context, we presented a white opaque oval dish (11 x
171 7.5 x 3.5 cm) filled with dried mealworms to each of the starling groups once a day for 12 days
172 between November 14th and December 7th 2011. Dried mealworms are a highly desirable treat
173 to starlings, and the mealworm dish was small enough for a single starling to monopolize it. We
174 filmed each trial and scored all occurrences of any starling displacing another from the dish, as
175 well as the identities of the starlings involved, for ten minutes after the first bird started to feed
176 from the dish. To quantify starlings' dominance ranks we summed the total number of
177 displacements for each possible dyad in each starling group across the 12 feeding trials. We
178 then calculated each bird's David's score (Gammell et al. 2003; Boogert et al. 2006; de Vries et
179 al. 2006). David's scores take the proportions of wins and losses of the focal subject's

opponents into account, while also correcting for variation in interaction frequencies between dyads (de Vries et al. 2006). We refer the reader to Gammell et al. (2003) and de Vries et al. (2006) for a detailed description of the rationale underlying David's scores and the equations used to calculate them, and to Boogert et al. (2006) for an example of David's scores calculated for captive starlings.

Perching ranks

To assess dominance ranks in a perching context, we observed each starling group for 18 10-min sessions between November 10th and December 21st 2011. During each session, we scored all occurrences of any starling displacing another from the latter's perching location, as well as the identities of the displacing and displaced starlings. We focussed on perching displacements as Boogert et al. (2006) showed these to provide a robust measure of agonistic rank. To quantify perching ranks, we summed the total number of displacements for each possible dyad in each starling group across the 18 observation sessions, and calculated a David's score (see above) for each bird.

Demonstrator training

In February 2012, we trained two starlings from each group, one dominant and one subordinate, to open an opaque plastic grey or pink miniature 'rubbish bin' (HxWxL: 19 x 13 x 17cm) filled with dried mealworms by either pushing one section of the lid down (Push method), or by prying open the other section (Pry method; Figure 1). We trained birds to use the Push or Pry method by shaping them through successive approximation: initially the lid was taped such that the lid part to be interacted with was completely open in the desired orientation (i.e. pointing down for the Push method and pointing up for the Pry method) and the starlings to be trained could freely forage on the mealworms underneath. Once they had habituated to feeding from the Push or Pry part of the bin, we progressively closed the lid such that birds could only obtain mealworms by pushing down the front part of the lid (Push method) or lifting up the back part (Pry method). Each demonstrator was thus trained to use

only one of the two methods available to open the bin lids and access the mealworms underneath.

As we found previously in a different population of captive starlings (Boogert et al. 2006), these birds' dominance in terms of their foraging ranks did not significantly correlate with their perching ranks (Linear Mixed Effects Model including group as a random effect: t_{24}=1.32, P=0.20). We therefore selected demonstrators that had relatively high (dominant demonstrator) or low (subordinate demonstrator) ranks in both foraging and perching contexts. In group 1 these were two juvenile males, in group 2 the dominant demonstrator was an adult male and the subordinate was a juvenile female, and in groups 3 and 4 the dominant was a juvenile male and the subordinate a juvenile female. We moved demonstrators to a wire-mesh cage (122 x 71 cm and 138 cm high) located out of visual and auditory contact with the other starlings, and trained them in one of two groups: training group A consisted of dominant individuals from groups 1 and 2 and subordinates from groups 3 and 4, and training group B consisted of subordinates from groups 1 and 2 and dominants from groups 3 and 4. We presented training group A with grey-coloured bins and shaped them to use the Push method to access mealworms, while we shaped training group B to use the Pry method on pink bins. We thus trained one demonstrator from each starling group to Push and another demonstrator to Pry, each on a different-coloured bin, with the combination of demonstrator dominance and task solution counterbalanced between groups. Due to space, time and group size limitations, we did not take task colour into account when counterbalancing for demonstrator dominance and task solution; no birds were trained to open pink bins using the Push method or to open grey bins using the Pry method. However, in the diffusion experiment both grey and pink bins could be opened using both Push and Pry methods, and our analyses showed that bin colour did not significantly affect the results (see below).

We trained each demonstrator group twice a week for five to eight hours per training day. Training cages were equipped with perches, hay bedding, a bird bath, and ad libitum softened dog food and water. However, demonstrator starlings could obtain the highly desirable dried mealworms only by opening the novel foraging tasks, either by using the Push method on grey bins (training group A) or the Pry method on pink bins (training group B).

Demonstrators struggled to open the novel foraging task lids when they were fully shut. For the final training sessions and the diffusion experiment, we therefore wedged the lids slightly open with transparent tape, creating a gap of ca. 0.5 cm such that birds could not easily see the food, and still had to Push or Pry the lid open to access the mealworms. The diffusion experiment started once all demonstrators were reliably performing the task opening methods they had been trained on.

Diffusion Experiment

In March 2012, we presented each starling group (including demonstrators) in their home enclosure with one bin of each colour per bird. Group 1, containing 10 starlings, was thus presented with 10 pink bins and 10 grey bins, whereas group 2, containing 9 starlings, was presented with 9 bins of each colour, *etc*. Note that bins differed only in colour, and could thus be opened using both Push and Pry methods. To create distinctly coloured foraging patches, we arranged all bins of one colour in holes cut into a 1 x 1 x 0.1 m cardboard box (Figure 2). The locations of these foraging patches were counterbalanced between groups, such that the box containing grey bins was located at the front of the enclosure in starling groups 1 and 3, and at the back of the enclosure in starling groups 2 and 4. Each bin contained enough dried mealworms that depletion did not occur during any diffusion trial. Each diffusion trial lasted 90 minutes. Each starling group was presented with five experimental trials following the first trial in which any bird accessed the mealworms, resulting in a total of six trials across two to three test days for the novel task solutions to spread through each group. If starlings did not show interest in the novel foraging tasks during the first trial, we sprinkled dried mealworms on top of the foraging patches to encourage birds to approach the tasks. Groups received two to three trials per day, and were provided with softened dog food for at least an hour in between trials. We filmed each trial with two Panasonic SD80 cameras on tripods, one positioned at each end of the enclosure. From the video recordings, we scored the start and end times of each task solving bout, the solver's identity, the colour and location within the foraging patch of the bin being accessed, and the method (Push or Pry) used to solve the task.

None of the starlings in group 4 (including the demonstrators, surprisingly) ever interacted with any of the novel foraging tasks in the diffusion experiment. We therefore focus all our analyses on starling groups 1, 2 and 3, in which both novel foraging methods were adopted by all but four birds by the end of the sixth experimental trial (see Results and Fig. 3). The relationship between sample size and statistical power is not straightforward in an NBDA (Hoppitt et al. 2010a). However, the sizeable difference in posterior probabilities between the perching and feeding networks indicated that the diffusion of two methods through three groups was, in this case, sufficient to discriminate which network had better explanatory power (see Results). There were also sufficient data to estimate the strength of the social transmission effect with reasonable precision, as indicated by the confidence intervals (see Results).

Ethics statement

The experiments described in this study were approved by the University of St. Andrews' Animal Welfare and Ethics Committee (AWEC: 11/07/2011) of the School of Biology and adhere to the Association for the Study of Animal Behaviour Guidelines for the Treatment of Animals in Behavioural Research and Teaching. Starlings were caught under Scottish Natural Heritage Licence 12105 and maintained good health throughout this study, as certified daily by the NACWO and monthly by the university vet. None of the displacements observed to assess dominance ranks resulted in any physical injury. The presence of dominant birds did not impede subordinates' access to their maintenance diet, water, or experimental tasks used in the diffusion study, as the latter provided two tasks per bird in each group. Birds were re-habituated to foraging outdoors in temporary outdoor aviaries at their site of capture in June 2013 and subsequently released.

Statistical analyses

Network-based diffusion analysis (NBDA; (Franz & Nunn 2009)) infers social transmission of information if the order in which birds adopt a novel behaviour (Order of Acquisition Diffusion Analysis: OADA), or the times at which they do so (Time of Acquisition Diffusion Analysis: TADA), follows a social network (Hoppitt et al. 2010a). NBDA can also be used to test specific

hypotheses about the pathways of diffusion, by comparing the fit of models which include different social networks (Franz & Nunn 2009). We used the Bayesian extension of TADA that allows inclusion of random effects (Nightingale et al. in press). We treated the Push and Pry task solutions as distinct behavioural traits, and included a parameter representing the difference between solving rates using the two solving methods to allow for the fact that they appeared to differ in difficulty (with the Push method being easier than the Pry method). We included a group-level random effect with a hierarchical normal prior to take into account the fact that birds' asocial solving rates within each group might be correlated. We also initially included an individual-level random effect to account for the fact that the rate at which each individual solved the task using both methods might be correlated. However, this random effect was estimated to have little effect (variance estimated at < 0.1), so we dropped this random effect to improve the efficiency of the MCMC process. The prior distribution for each parameter was uniform, representing a lack of prior knowledge about the corresponding effects (see Appendix for details). We obtained posterior parameter estimates and performed model discrimination using a Reversible Jump Markov Chain Monte Carlo algorithm (RJMCMC: (Green 1995)). We initially included individuals' sex, age (note that our study population did not include adult females), body condition (expressed as the regression residuals of body mass as a function of wing length), foraging ranks and perching ranks, as well as the colour of the bin accessed by each bird, in our models. However, the posterior estimates of these parameters were always negligible, so individual characteristics and bin colours were not included in our final models.

We first analysed a "condensed" dataset (i.e. the standard dataset for NBDA) to test whether individuals' first time to use the Push and/or Pry methods could be explained by the foraging network **F**, a "weighted" foraging network $\mathbf{F}_w$ in which the ratio of group members' use of Push verses Pry methods was taken into account, the perching network **P** or a homogenous network **H** that assumed equal transmission between all group members. We then analysed the "full" dataset to test whether individuals' repeated use of Push and Pry methods could be predicted by any of the abovementioned networks.

NBDA analysis of starlings' first use of Push and Pry methods

We parameterised the model using the alternative parameterisation suggested by Nightingale et al. (in press) facilitating the setting of priors (see Appendix) for the Bayesian NBDA, while the Bayesian NBDA in turn facilitates the inclusion of random effects. For the NBDA models in this analysis, we adopt the additive model proposed by Hoppitt et al (2010b). We specified that the rate at which individual *i* solves the task using method *a* (e.g. Push), $\lambda_{a,i}$, is given by

$$\lambda_{a,i} = \left(\lambda_0 \exp\left(LP_i\right) + s' \sum_{j=1}^{N} A_{ij} z_{a,j} \right) \left(1 - z_{a,i}\right)$$

where λ_0 is the baseline, or asocial, rate of solving, s' gives the rate of social transmission per unit of connection to informed individuals, A_{ij} gives the connection from individual *j* to individual *i* in the social network being used, $z_{a,j}$ is the status of individual *j* with respect to method *a* (1= learned method *a*; 0= not learned method *a*), and LP_i is a linear predictor determining the effects of the other variables, such as random effects, in the model. Here $s' = s\lambda_0$ in the standard parameterisation for NBDA. We extended the parameter space to include multiple *s* parameters corresponding to the different rates of social transmission per unit of connection subserved by the four different social networks (see below).

Model comparisons

Let θ denote the set of parameters such that $\theta = \{\lambda_0,\ s',\ s'',\ s''',\ s^{1V}, \eta\}$ where λ_0 denotes the baseline or asocial learning rate, s' represents social transmission through the foraging social network **F**, s''represents social transmission through a homogenous social network **H** in which all group member associations were set to 1, s''' denotes social transmission through a social network $\mathbf{F}_w$, derived from the foraging association network **F** where, in the hazard function for method *a* (Push), each association **F**[i,j] was multiplied by a weight $w_{a,j}w_j$ to obtain $\mathbf{F}_{w,a}[i, j]$. The weight $w_{a,j}w_j$ was calculated as the ratio of the number of times *j* solved the task using the Push method to the number of times *j* solved the task using the Pry method. Likewise,

in the hazard function for method *b* (Pry) each association **F**[i,j] was multiplied by a weight $w_{b,j}$, the ratio of the number of times *j* solved the task using the Pry method to the number of times *j* solved the task using the Push method, $1/w_j$ to obtain $\mathbf{F}_{w,b}$[i, j]. In each case it was assumed that individual *i* would be affected by the task solving method-preferences of *j* by an amount proportional to the strength of the association between them, and the strength of the solving method preference of *j*. Parameter s^{1V} represents social transmission through the perching social network **P** and parameter η, a binary variable, accounts for the overall difference in the rate at which individuals solved the tasks when using the Push method (η =1) as compared to using the Pry method. All parameter values were estimated by the model. Random effects at the group level were denoted by ε_1, ε_2, and ε_3.

Table 1 describes the nine models we compared to test which would explain the diffusion of the Push and Pry methods through the three starling groups best. Model 1 represents the hypothesis that starlings learned to solve the novel foraging task asocially and at a constant rate. The model that received the highest posterior support after employing the RJMCMC model discrimination algorithm was model 9, which includes the asocial learning rate parameter λ_0, the perching network parameter s^{1V} and the differential-foraging-rate parameter η (see Results).

Six additional models were then considered, expanding the best model from Table 1, to test whether social effects generalised between the two task solving methods or not (see below and Table 2). In addition, models 10, 11 and 12 contain a constant asocial baseline rate (λ_0), whilst models 13, 14 and 15 account for the fact that the asocial rate of learning may increase or decrease over time (indicated by the α (or 'shape') and β (or 'rate') parameters), for example as a result of decreasing neophobia over time (Hoppitt et al. 2010b; see Table 2). For these models, we adapted the multi-option version of NBDA used by Atton et al (2012) in an OADA context to be used in a TADA context. Using the same notation as above, we introduce the following terms into the hazard function, $\lambda_{a,i}$, :

$$s_s' \sum_{j=1}^{N} A_{ij}\, z_{a,j}(t),$$

$$s'_d \sum_{j=1}^{N} A_{ij}\, z_{b,j}(t),$$

Parameter s'_s denotes the effect of a focal individual learning a task solution from group mates that solve the task using the same task solution (s = same), and s'_d represents the effect of learning a task solution from group mates that solve the task using the alternative method (d = different). The term $z_{a,j}$(t) represents a binary variable which equals 1 if individual *j* has solved the task using the same (Push) method, prior to time *t*, while the term $z_{b,j}$(t) represents a binary variable which equals 1 if individual *j* solved the task using the alternative (Pry) method.

We also introduce the term $\phi z_{b,j}(t)$ into the linear predictor LP_i for $\lambda_{a,i}$, and the equivalent terms into $\lambda_{b,i}$ with $\phi' z_{a,j}(t)$ replacing $\phi z_{b,j}(t)$. Parameter ϕ gives the effect on the rate at which *i* solves the task using the Push method of this same individual *i* having previously solved the task using the Pry method. The opposite effect is denoted by ϕ'. Similarly, $z_{b,i}(t) = 1$ if an individual *i* has solved the task using the Push method prior to time *t*. The hazard function for method *a* (Push) is:

Field Code Changed

$$\lambda_{a,i}(t) = \left(1 - z_{a,i}(t)\right)\left(s'_s \sum_{j=1}^{N} A_{ij}\, z_{a,j}(t) + s'_d \sum_{j=1}^{N} A_{ij}\, z_{b,j}(t) + \lambda_0 + \phi z_{b,i}(t) \right)$$

and for method *b* (Pry):

$$\lambda_{b,i}(t) = \left(1 - z_{b,i}(t)\right)\left(s'_s \sum_{j=1}^{N} A_{ij}\, z_{b,j}(t) + s'_d \sum_{j=1}^{N} A_{ij}\, z_{a,j}(t) + \lambda_0 + \acute{\phi}' z_{a,i}(t) \right)$$

We consider the situation where $s'_s \neq s'_d$, $s'_s = s'_d$, and $s'_s = s'_d = 0$.

The model likelihoods follow those given by Hoppitt & Laland (2013).

To give an intuitive estimate of the importance of social transmission (Allen et al. 2013), for the model that received the highest posterior support, the estimated number of task solves that occurred by social transmission T_s, where there are N solving events, was calculated as:

$$T_s = \sum_{t=1:N} \frac{s \sum_{j \neq i} A_{ij} z_j(t)}{s \sum_{j \neq i} A_{ij} z_j(t) + 1}.$$

The proportion of solves by social transmission was then obtained by dividing T_s by the total number of solves, N.

NBDA analysis of starlings' repeated use of Push and Pry methods

We went on to use the Bayesian NBDA model specified above to test whether the starlings affected each other's use of the Push and/or Pry methods once they had acquired these task solutions and used them in repeated foraging bouts. We classified a foraging bout as foraging activities by more than one individual at the same time, with no more than 300 seconds between consecutive foraging activities. For each foraging bout, we analysed only the first time each group member used the Push and Pry methods. Each foraging bout was treated as a separate diffusion in the NBDA.

Table 3 describes the eight models we considered for this analysis. The models contained two new parameters in addition to those in Table 1: ϱ accounts for the effect of task solves by a trained demonstrator on the overall rate at which subsequent task solves occurred, and ζ accounts for the effect of the number of previous task solves by individual *i* on *i*'s subsequent task solves, or in other words: Did the frequency of solving a task in general (i.e. regardless of the solving method used) influence an individual's propensity to solve the task again?

Results

Starlings' first use of Push and Pry methods

All individuals in the three starling groups adopted the Push method, and the great majority (i.e. group 1: 8/10, groups 2 & 3: 8/9 starlings) adopted the Pry method to access the mealworms in the novel foraging tasks by the end of the diffusion experiment (see Fig. 3). Except for the Push demonstrator in group 1, none of the previously trained demonstrator birds (indicated with squares in Fig. 3) were the first of their flock to start solving the tasks.

The best-supported model was model 9 (Table 1), which provides strong evidence that social transmission followed the perching network within each starling group (posterior probability= 1; see Table 4 for parameter estimates). However, when we considered six extensions of this best-fitting model (see Table 2), the model emerging with the strongest support after model discrimination on models 9-15 was model 12, with a posterior probability of 0.97, while model 9's posterior probability then became 0.03. The greater support for model 12, in which social effects generalised between Push and Pry methods relative to models 10 and 13 (with posterior probabilities of 0), in which social effects were specific to each option, suggests that starlings did not learn specific methods of solving through observation. The posterior parameter estimates for model 12 (see Table 5) suggest that the rate of social transmission per unit of perching association, relative to the baseline rate of asocially learning either task solution, was 6.67. This means that for every unit of perching connection to informed individuals using the Push or Pry method, the rate at which a naive individual first solved the task using either method increased by almost seven times the baseline asocial rate of learning. The estimate for the baseline asocial learning rate suggests that starlings solved a task asocially every 1/0.0001=10.000 seconds. The estimate of the η parameter suggests that starlings tended to be 5.4 times (i.e. 1*exp(1.68)) faster to first solve using the Push method than the Pry method. The ϕ estimate suggests that previously solving using the Pry method generalised to increase the rate of solving using the Push method by the same individual by 0.40, whereas previously solving using the Push method increased the solving rate using the Pry method by the rather small amount of 0.09 (i.e. the estimate for ϕ'). The proportion of solves that occurred via social transmission is estimated to be 0.13.

Starlings' repeated use of Push and Pry methods

Across the three starling groups, we analysed a total of 46 foraging bouts in which birds used the Push and/or Pry methods. Across these foraging bouts, starlings solved tasks a total of 728 times in group 1, 835 times in group 2, and 433 times in group 3. However, for each foraging bout, we analysed only the first time each group member used the Push and Pry methods, as described above. The model that received the highest posterior support of 0.97 was model 21 (see Table 3), which contained a social effect parameter s'' (based on the homogenous social network **H**), a parameter accounting for the effect of the number of previous task solves, ζ, and a baseline rate parameter, λ_0. The posterior parameter estimates for this model (see Table 6) suggest that for every unit of connection to task-solving individuals, the rate at which an individual solved tasks increased by 1.01 times the baseline asocial rate of solving. The estimate for the asocial baseline rate suggests that the average time for an individual to solve a task asocially within a bout was 333 seconds (i.e. 1/0.003). When scaled by the social parameter, this becomes 1/((1.01+1)0.003)=166 seconds, corresponding to the average time an individual would take to solve the task once another bird in the group had done so in that bout, 110 seconds when two others had solved; 83 seconds when three other birds had solved, and so on. Finally, the ζ estimate suggests that increasing the number of times that an individual solved the task previously by one, increased the rate of that *same* individual solving the task again by the very small amount of 0.0004 (i.e. exp(-7.78)). The proportion of solves that occurred via social transmission is estimated to be 0.37. The analysis with the multi-option NBDA models yielded posterior estimates that were close to zero.

Discussion

In this study, we assessed whether the spread of two novel foraging task solutions in three starling groups could be explained by individuals' characteristics and their patterns of association in different social networks. We found clear evidence for social learning: for every unit of social network connection to informed individuals solving the novel foraging task, the rate at which a naïve individual started to solve the task was almost seven times the asocial learning rate. However, starlings did not appear to copy the specific foraging method used by

their knowledgeable flock mates, suggesting that they socially learned to extract food from the novel foraging tasks, but not specifically how to do so. Strikingly, the pattern of information flow through the starling populations, in what was a foraging task, was better predicted by the association network constructed based on the birds' perching behaviour than the corresponding foraging network. In contrast, once birds had acquired the task solution(s), their subsequent task solves followed the homogeneous social network, in which all connections between individuals were set to 1. Individuals' task solves, once they had acquired the Push and/or Pry methods, were thus facilitated by the presence of group mates solving tasks, regardless of the identity of those group mates.

Our finding that the perching network rather than the foraging network best explained the spread of the novel foraging task solutions through the starling groups is surprising and seemingly counterintuitive. We previously showed that a perching network could not explain the spread of novel foraging tasks solutions in captive starling groups (Boogert et al. 2008), and suggested that this might be due to the relatively small group sizes (five birds/group) and test enclosures: as all individuals were continuously in relatively close proximity to all other group members, the birds in our previous study might not have had as much freedom to express perching preferences as in our current study, where both group and enclosure sizes were double those used by Boogert et al. (2008). Our current findings suggest that perching networks, when constructed for slightly larger flocks with more perching space, tap into who starlings attend to when they learn, which seems to be a function of whom they preferentially associate with in a non-foraging context. Conversely, networks based on normal foraging behaviour might not be as informative; when captive starlings, held in comparatively small laboratory enclosures, feed under normal circumstances, they may have little opportunity or need to express any preferences for feeding with specific birds, and are merely content to feed in the company of conspecifics. If so, then association networks based on normal foraging behaviour may provide little information as to who they would look to to acquire the solution to a novel foraging task. Under these circumstances, perching networks provide a more reliable indication of the spread of novel behaviours, especially as group members could have a clear and relatively close-up view of both novel foraging patches on the floor of the enclosure from

all perches available. It is possible that this pattern is reversed amongst birds in their natural environment, where foraging behaviour might better represent social preferences, and naturally occurring perches might not necessarily be situated nearby, or with a clear view of, natural foraging patches. In addition, whereas our captive starlings socially learned to open tasks using either method, regardless of the specific method previously used by their perching associates, perhaps the copying of specific foraging methods is also facilitated by more meaningful foraging social networks in the wild. A comparison of the ecological significance of different social networks in natural populations versus those constructed in captivity provides an interesting venue for future research. Furthermore, recent research shows that in shoals of three-spined sticklebacks, foraging patch discoveries are more likely to follow the social network in structured than in open environments (Webster et al. 2013). We are currently investigating whether presenting captive starling flocks with a more structured foraging environment, in which individuals can forage out of view of group mates, leads to foraging networks with more ecological significance.

Interestingly, while the perching network best explained birds' first adoption of the Push and/or Pry methods, birds' subsequent use of these novel task solutions in repeated foraging bouts was predicted by a homogenous social network, suggesting that focal individuals were more inclined to solve tasks while others were doing so, irrespective of the identity of these foraging companions. This finding raises the interesting possibility that animals tap into different social networks depending on their priorities: when needing to acquire specific foraging information that requires close spatial proximity, they might show directed social learning and attend to familiar group members that show social tolerance. Conversely, once the information has been acquired, individuals' priorities seemingly shift to using it (e.g. novel foraging task solutions) in the safety of the group, and the identity of the group members then becomes less important.

We estimated that ca. 13% of all task solves occurred through social transmission, which suggests that the remainder of task solves were either affected by social processes not captured by the social networks under study, or by asocial processes. Surprisingly, there was no strong evidence for an effect of individuals' sex, age, body condition, and dominance ranks on

their rates of acquiring or using the novel task solutions. It is possible that these results would have been different had our study population included adult females. However, there is no a priori reason to predict adult female starlings to disproportionally affect the origin or spread of novel task solutions through the captive flocks. This contrasts with findings in several other species. In shoals of guppies, for example, females were more innovative than males (Laland & Reader 1999) and innovations spread faster through female than through male subgroups (Reader & Laland 2000), while in wild meerkat groups, subordinate adult males were most likely to innovate (Thornton & Samson 2012) and juveniles were more likely to socially learn than adults (Thornton & Malapert 2009). In birds, problem-solving performance was not affected by sex or age in wild great tits (Cole et al. 2011), while juvenile females and subordinate males were most likely to learn socially in blue tit flocks (Aplin et al. 2013). In captive flocks of starlings, individuals of high perching rank were most likely to innovate the solutions to a series of novel foraging tasks (Boogert et al. 2008). In contrast to Boogert et al. (2008), here we trained two birds of opposite dominance ranks in each flock to perform the Push and Pry methods, with the aim of 'seeding' the diffusions in the flocks and testing whether their group mates preferentially learned from the dominant or subordinate demonstrator. This design was inspired by studies on domestic hens (Nicol & Pope 1999) and chimpanzees (Horner et al. 2010), in which individuals were found to copy dominant rather than subordinate demonstrators. Although we did not start the diffusion experiment until all demonstrators reliably performed the task solutions on which they had been trained, only one of the demonstrators was actually the first to start solving when presented with the tasks in their home flocks (see Fig. 3). It would seem that social context (i.e. training vs home flock) affected the demonstrators' performance. A previous study on Indian mynahs found that individuals were significantly slower and less likely to solve a novel foraging task when tested in pairs or small flocks as compared to when tested alone (Griffin et al. 2013). Similarly, Carib grackles were significantly slower to contact a novel foraging task when two conspecifics were watching in an adjacent cage (Overington et al. 2009). These results have been interpreted as negotiation over risk; when encountering novel foraging situations, it might be safer to leave group members to innovate and wait for an opportunity to scrounge (Overington et al. 2009; Griffin et

al. 2013). However, as the demonstrators in our study had been trained to solve the exact same foraging tasks as those presented in the diffusion experiment, it seems unlikely that they perceived the bins as novel items that were "risky" to interact with. Instead, the demonstrators may have delayed performing their acquired task solutions to avoid displacement and food theft by group mates. Grackles were slower to start dunking hard dog food pellets in water when the perceived risk of food theft by neighbouring conspecifics was higher (Overington et al. 2009). Perhaps our demonstrators perceived their home flock, containing eight to nine other birds as compared to the three other birds in the training flock, as a relatively competitive environment to perform their newly acquired foraging skills in. Indeed, once birds started extracting mealworms from the bins, displacements by group mates were regularly observed.

There are two valuable lessons to be taken from our study. First, it demonstrates the power of NBDA to detect social learning, and confirms that newly learned information flows along pathways of association in relevant social networks. However, second, the study also shows that which network best predicts social information flow will depend very much on the context. It would seem that when animals need to learn new tasks, they may look to familiar individuals or close associates as a source of knowledge, and that alternative networks vary in the extent to which they accurately capture these associations. Conversely, once they have acquired the task, animals may be less discriminating in their choice of social partners. It would be a valuable extension to ascertain whether these conclusions hold up in natural animal populations.

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Appendix: NBDA Priors

We set vague priors on the social effect parameters to reflect the lack of prior information about rates of social transmission among starlings in this context, following Nightingale et al. (in press). We first estimated the fastest plausible time we might expect a starling to solve a novel foraging task, assuming all other individuals to whom it was connected were informed individuals, as t_{max}= 12.5 seconds, based on the shortest latency for a captive starling to solve a novel foraging task in a social context as observed by Boogert et al. (2008). The average connectedness (total connection to other individuals), k, is 0.4 (for all the networks considered), so the maximum plausible rate of social transmission per unit of association would be $\frac{1}{k*s_{max}}$ =0.2. Therefore, for the social effect parameters, we specified a Uniform prior $s \sim U(0, 0.2)$. For the model discrimination, an additional prior for the social effect was selected $s \sim U(0, 3)$ to determine whether there was any sensitivity to widening the variance of the prior selected, and found this did not affect the posterior model probabilities. The exact width of the priors for other parameters is not critical for our inference about the presence/ absence of social transmission, since these priors were the same for models with and without social transmission.

We set a similar uniform prior for the baseline parameter, λ_0, again using the maximum plausible average latency for a starling to solve the task, 20114 seconds (again based on the data in Boogert et al. 2008), and then using the inverse of this as the maximum plausible asocial learning rate. For the method effect parameter, η, a Normal prior was specified which allows both negative and positive values. The variance for this prior was set as 1 such that $\eta \sim N(0,1)$. Finally, a Normal prior was specified for the ϕ and ϕ'parameters such that $\phi, \phi' \sim N(0,1)$ and a Uniform prior was specified for the hyperparameters α and β such that $\alpha, \beta \sim U(0,10)$.

FIGURES

Figure 1. Bins used as novel foraging tasks in the diffusion experiment. Demonstrators were trained either to push down the sloped lid section (Push method) or to pry open the flat lid section (Pry method) to access the dried mealworms in the bins. Push demonstrators were trained to access grey bins, and Pry demonstrators were trained to access pink bins. Grey and pink bins were identical apart from their colour, and could thus be opened using both Push and Pry methods in the Diffusion Experiment.

Figure 2. Starlings from group 1 (a) and group 2 (b) solving the novel foraging tasks while standing on the cardboard boxes that organized the bins into two distinctly coloured foraging patches.

Figure 3: Diffusion curves for starling groups 1 (a), 2 (b) and 3 (c). Latency (in seconds) to first use the Push/Pry method is indicated on the x-axis, and the rank order in which individuals solved the task is indicated on the y-axis (i.e. the first bird in a group to solve the task has a 'solver index' of 1, etc). Diffusion of the Push method is represented by a solid line, and diffusion of the Pry method is indicated with a dashed line. The unique numerical id for each solver within each starling group is indicated on the plots, and squares indicate the starlings that had been trained as demonstrators before the start of the diffusion experiment.

TABLES

Table 1: Models considered to explain starlings' first use of the Push and Pry methods

Table 2: Extensions of the best-fitting model to explain starlings' first use of the Push and Pry methods

Table 3: Models considered to explain starlings' repeated use of the Push and Pry methods

Table 4: Posterior parameter estimates and 95% credible intervals for the best-fitting model of individuals' first use of the Push and Pry methods in the three starling groups.

Table 5: Posterior parameter estimates and 95% credible intervals for the best-fitting extended model (based on multi-option OADA) of individuals' first use of the Push and Pry methods in the three starling groups.

Table 6: Posterior parameter estimates and 95% credible intervals for the best-fitting model of the repeated use of the Push and Pry methods in the three starling groups. Note that the estimates for ζ are provided in natural logarithms.

Table 1

Table 1

Model	Parameters
1	λ_0
2	λ_0, s'
3	s',η
4	λ_0, η
5	λ_0, s', η
6	λ_0, s', η, $\varepsilon_1, \varepsilon_2, \varepsilon_3$
7	λ_0, s'', η
8	λ_0, s''', η
9	λ_0, s^{IV}, η

Table 2

Table 2

Model	Parameters
10	$s_s^{IV}, s_d^{IV}, \lambda_0, \phi, \phi', \eta$
11	$\lambda_0, \phi, \phi', \eta$
12	$s^{IV}, \lambda_0, \phi, \phi', \eta$
13	$s_s^{IV}, s_d^{IV}, \phi, \phi', \alpha, \beta, \eta$
14	$\phi, \phi', \alpha, \beta, \eta$
15	$s^{IV}, \phi, \phi', \alpha, \beta, \eta$

Table 3

Table 3

Model	Parameters
16	λ_0
17	λ_0, s'
18	λ_0, s', ϱ
19	λ_0, s', ζ
20	λ_0, s''
21	λ_0, s'', ζ
22	λ_0, s'''
23	λ_0, s^{IV}, η

Table 4

Table 4

Parameter	**Mean (95% credible interval)**
social transmission effect $s = \frac{s^{IV}}{\lambda_0}$	1.98 (0.07, 7.67)
constant baseline asocial learning rate λ_0	7.94×10^{-5} (2.62×10^{-5}, 1.41×10^{-4})
bias towards Push method of solving η	1.75 (1.72, 1.82)

Table 5

Table 5

Parameter	**Mean (95% credible interval)**
social transmission effect $s = \frac{s^{IV}}{\lambda_0}$	6.67 (3.97, 8.86)
constant baseline asocial learning rate λ_0	0.0001 (3.4×10^{-6}, 3.3×10^{-4})
bias towards Push method of solving η	1.68 (1.63, 1.77)
acceleratory effect of learning Pry on subsequent solving rate using Push ϕ	0.40 (0.25, 0.60)
acceleratory effect of learning Push on subsequent solving rate using Pry ϕ'	0.09 (0.085, 0.086)

Table 6

Table 6

Parameter	Mean (95% credible interval)
social transmission effect $s = \frac{s''}{\lambda_0}$	1.01 (0.233, 4.716)
baseline asocial learning rate $\boldsymbol{\lambda}_0$	0.003 (0.0004, 0.004)
effect of # previous solves on current solves ζ	-7.78 (-9.85, -5.79)

Figure1

Figure2

Figure 3a
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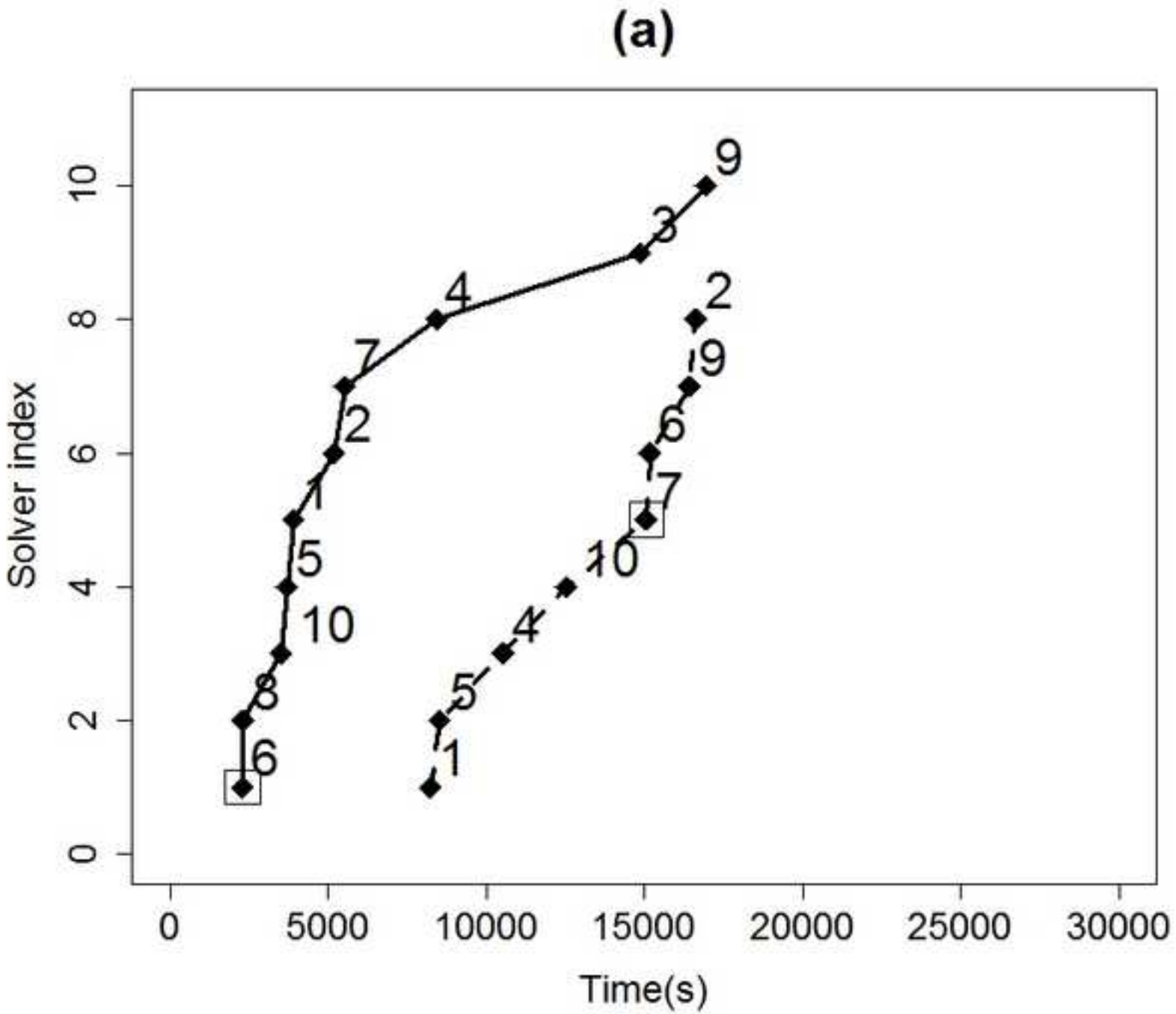

Figure 3b
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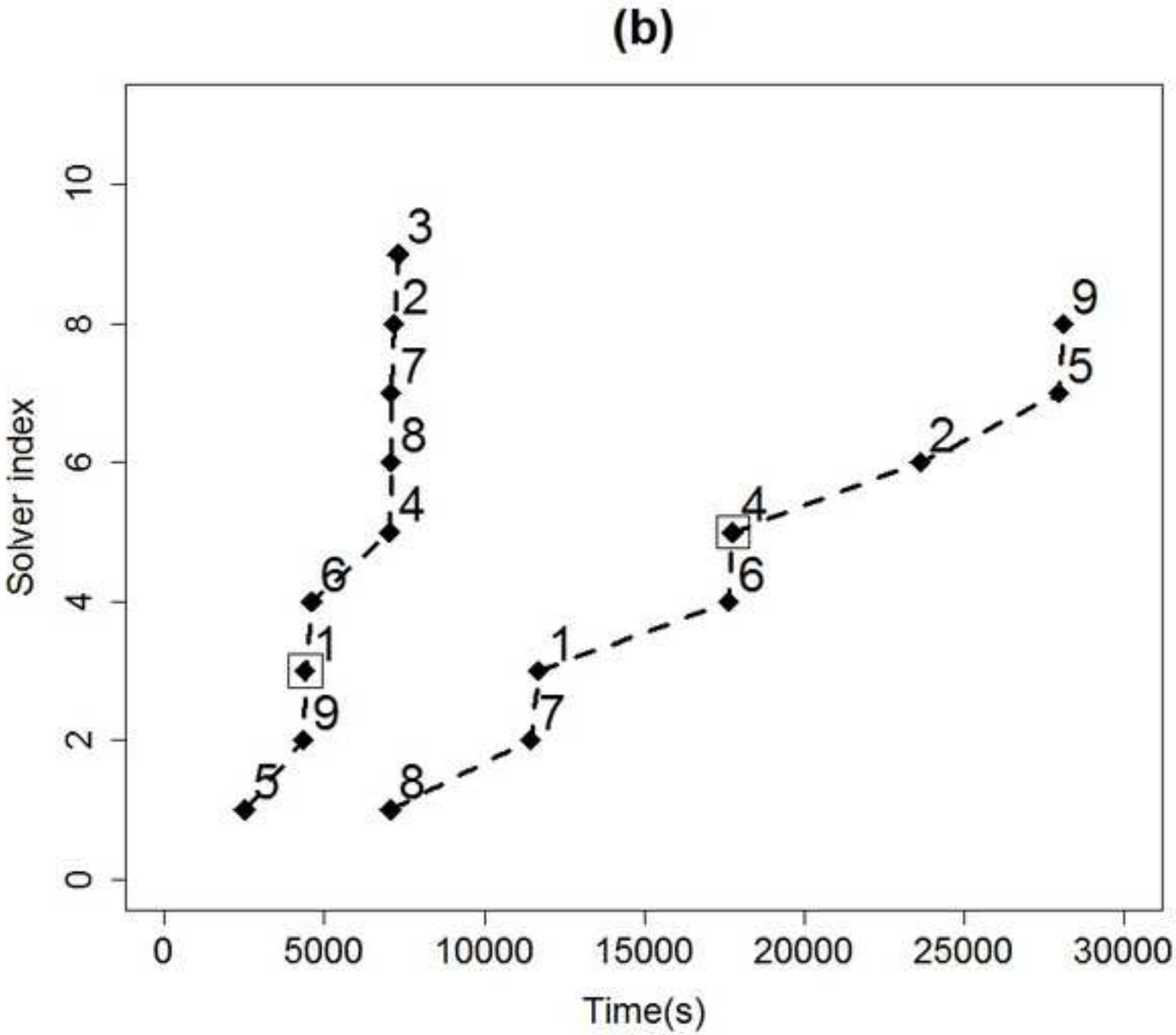

Figure 3c
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